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Research Article

Changes in morpho-physiological and yield attributes of *Sesamum indicum* under waterlogging at different growth stages

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ABSTRACT

To understand the responsive nature to excess water, a pot experiment was conducted at different growth stages of sesame (*Sesamum indicum* L. cv. BARI Til-4). The waterlogging stress at each stage was set to three durations, viz. 2, 4, and 6 days. Twelve different treatment combinations were replicated three times and arranged in a completely randomized design. Different morpho-physiological and yield parameters were measured after the completion of the longest stress duration (6 days). The data revealed that sesame is vulnerable to excess water conditions, and the sensitivity is positively correlated with the stress duration. Plant biomass, leaf area, SPAD value, and the yield attributes recorded are observed to be declined with the increment of stress duration. Another important finding is that among the three growth stages of sesame, the reproductive stage is the most sensitive stage, which hardly withstands waterlogging. The stress at the vegetative stage affect yield parameters minimally.

Introduction

Waterlogging is one of the most devastating abiotic stresses that negatively affect crop production. More than 16% of the cultivated area is globally prone to waterlogging exposure (Ploschuk et al., 2018). In addition, climate change is accelerating the erratic incidence of precipitation, making the situation worse for global crop production. Many natural and anthropogenic causes, such as heavy rainfall, flash flood, unplanned irrigation or drainage, dam failure, etc., are responsible for causing waterlogging (Anee et al., 2019). The effect of waterlogging stress varies depending on crop species, duration, soil type, water level, plant growth stage, and other environmental factors (Hasanuzzaman et al., 2017). Different types of morpho-physiological, anatomical, and biochemical alterations such as growth reduction, leaf senescence, chlorosis, wilting, flower and fruit dropping, delay in maturity, disease infestation, etc., are some of the most common phenomena caused by waterlogging stress (Jia et al., 2021; Pan et al., 2021). Oxygen availability gets reduced proportionately to the magnitude of waterlogging, resulting in hypoxia or oxygen deficiency for short-duration stress and anoxia or absence of oxygen for longer durations (Olorunwa et al., 2022). Plant anaerobic respiration occurs due to a lack of oxygen which reduces energy and gas exchange leading to cell death in crops sensitive to waterlogging and reduced yield (Gibbs and Greenway, 2003; Pan et al., 2021). To minimize the losses, it is necessary to find out the possible mechanisms of plants under waterlogging and to develop varieties tolerant to waterlogging.

Sesame (*Sesamum indicum* L.) is the queen of oilseed crops globally and is categorized as healthy food, especially in Asian countries (Myint et al., 2020). According to FAOSTAT (2021), more than

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six million tons of sesame seeds were grown globally in approximately 12 million hectares of land, of which almost 97% of production belongs to Asia and Africa. Sesame is cultivated during the summer season in tropical and subtropical regions and hence faces several environmental adversities that restrict sesame cultivation and cause yield loss. Especially due to its susceptibility to waterlogging, farmers are losing interest in cultivating sesame. This poses a threat to national oil production, and a large amount of foreign currency is paid out to meet the demand. Therefore, it’s a prime need to research on developing high-yielding varieties of sesame tolerant to environmental constraints like drought, waterlogging, salinity, etc., as sesame is cultivated during the monsoon it is very likely to get exposed to waterlogging. Several studies have demonstrated different sesame genotypes’ waterlogging-induced growth and yield reduction.

Variations in growth stages, stress duration, water level, and genotypes of waterlogging stress have been documented to affect sesame growth and yield negatively. Linh et al. (2021) screened five sesame varieties for waterlogging tolerance and reported a time-dependent reduction of growth and yield parameters. A growth stage-dependent study with sesame revealed that at vegetative and flowering stages, the plant height, stem diameter, and chlorophyll (chl) content were reduced upon exposure to waterlogging for 2 and 3 days (Jung et al., 2019). Despite several similar literatures on sesame under waterlogging, there needs to be more information on duration and growth stage-dependent studies with sesame cultivars. And as an oilseed crop with the scope to be cultivated both in the tropics and sub-tropics, it is necessary to conduct in-depth studies of sesame responses and mechanisms under waterlogging stress. Therefore, this experiment was designed to understand sesame’s duration-dependent responses at different waterlogging stages.

Materials and Methods

Experimental Materials, Treatments, and Design

Clean and uniform seeds of sesame (*Sesamum indicum* cv. BARI Til-4) were sown in pots (14 L) and provided with well-prepared soil containing recommended doses of manures and fertilizers. Three different durations (2, 4, and 6 days) of waterlogging were considered at three growth stages: vegetative, reproductive, and maturity stages. Twenty-one days after sowing (DAS) was considered as the starting of vegetative stage, for the reproductive and maturity stages; it was 35 and 55 DAS, respectively. Water was added to create an anoxic condition by maintaining a height 3 cm above the soil level. After completion of treatment, water was drained out from the pots and irrigated as required for the rest of the time. For every three stages, a respective control was irrigated regularly as required, and data were collected after completing the longest waterlogging treatment at each stage. Pots were arranged in a completely randomized design consisting of 12 waterlogging treatments in three replications.

Measurement of Crop Growth Parameters

The height of plants was recorded from the ground level up to the tip of the leaf in centimeters (cm) using a measuring scale. The average height of five plants was considered as the plant height for each pot.

Three sample plants were uprooted from each pot randomly and washed in water. Then the plants were weighed in a balance and averaged to have fresh weight (FW) plant^{-1}. Three sample plants, after weighing for FW was dried in an electric oven, maintaining 60 °C for 48 hours. Then weighed in an electric balance and averaged them to have dry weight (DW) plant^{-1}. The average number of leaves from five plants was considered as the total number of leaves plant^{-1}.

The leaf area plant^{-1} was determined by measuring the length (cm) of 5 leaves, and counting the total number of leaves per plant, applying the following equation, $S=0.3552\times C^2$, where S=leaf area (cm^2) and C=leaf length (cm) and then multiplying the leaf area by the total number of leaves per plant to obtain the total leaf area plant^{-1} (cm^2).

Measurement of Leaf Greenness

Three leaves were randomly selected from each pot. The top and bottom of each leaflet were measured with Soil-Plant Analysis Development (SPAD) meter as SPAD value and then averaged.

Determination of Yield

The total number of capsule plant^{-1} was counted from five randomly selected plants and then averaged. Ten capsules from each pot were selected, and seeds were counted from each capsule and then averaged. One thousand clean sun-dried seeds were counted from the sample plants' seed stock and weighed using an electronic balance.

The grains were separated by threshing, and the plants were sun-dried and weighed. The biological yield was calculated by using the following formula:

Biological yield = Grain yield + Straw yield.

Statistical Analysis

The data obtained for different parameters were statistically analyzed using XLSTAT v. 2015 software (Addinsoft, 2016), and mean separation was done by LSD at a 5% level of significance.

Results and Discussion

The plant height showed no significant changes during the vegetative stage of seedling growth after waterlogging. But it reduced significantly at the reproductive stage when waterlogged for 4 and 6 days. At maturity, plant height decreased by 10 and 17% in plants waterlogged for 4 and 6 days, respectively, compared to the control plants (Fig. 1A).

As plant height showed little changes under waterlogging at the vegetative stage, there was also a lesser effect on above-ground FW plant^{-1}, except the plants were waterlogged for 6 days. But, in the case of the reproductive stage, FW reduced by 33, 50, and 54% after waterlogging for 2, 4, and 6 days, respectively. At maturity, 4, and 6 days of waterlogging duration reduced their FW by 35 and 36%, respectively (Fig. 1B).

As shown in Fig. 1C, DW remarkably reduced in plants waterlogged at the reproductive stage, but at the vegetative stage only affected the longer duration (6 days) of waterlogging treatment with a 37% reduction. However, plants waterlogged only for 4 and 6 days at maturity showed 40 and 50% lower DW, whereas waterlogging for 2 days was about 5% higher (Fig. 1C).

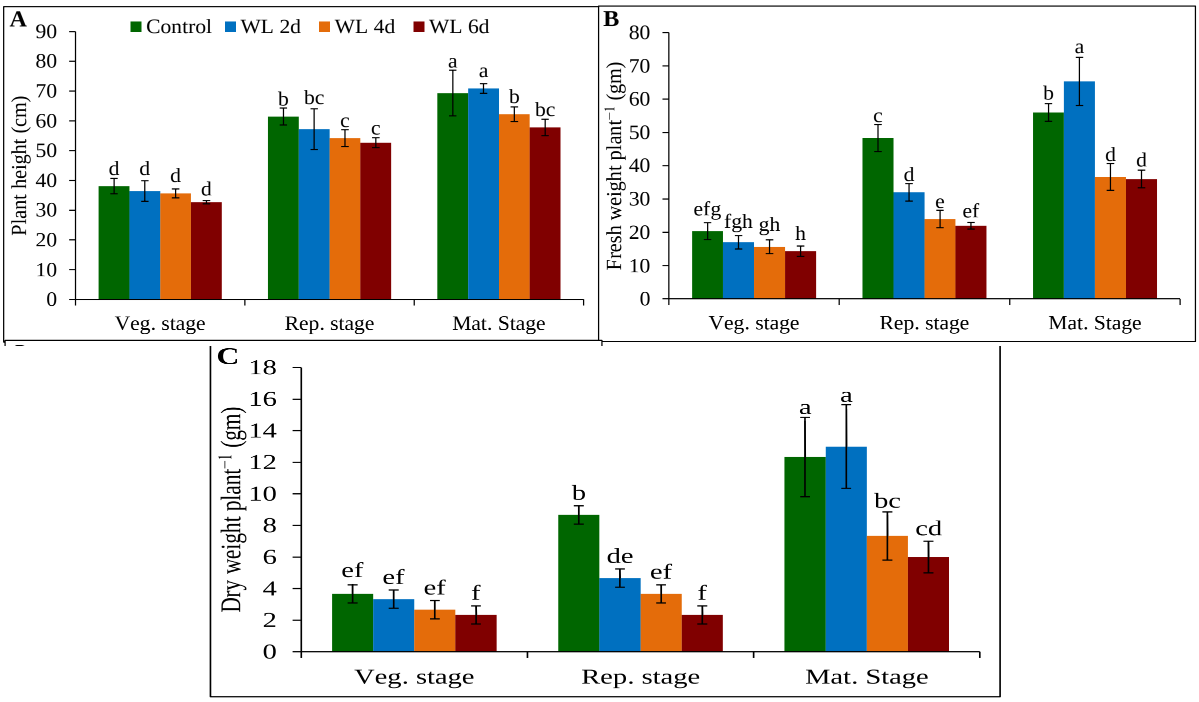

Fig. 1. Plant height (A), above-ground fresh weight (FW) plant^{-1} (B), and above-ground dry weight (DW) plant^{-1} (C) of sesame as affected by waterlogging stress at different growth stages. Mean (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

Significant reduction of leaves plant^{-1} has been observed in plants waterlogged either during the reproductive stage or maturity stage. Waterlogging treatments during the reproductive stage showed a lower number of leaves plant^{-1} by 44, 55 and 59% at 2, 4, and 6 days of waterlogging, respectively, compared to the corresponding well-drained plants (Fig. 2A). Plants waterlogged for 4 and 6 days at maturity stage showed a reduced number of leaves plant^{-1}, but higher in plants waterlogged for 2 days.

Though the leaf numbers were not significantly affected by waterlogging during the vegetative stage, leaf area reduced remarkably in the plants waterlogged for 6 days at this stage (Fig. 2B). This experiment also showed a marked reduction of leaf area by 30, 71, and 77% at the reproductive stage and 11, 70, and 76% at maturity stage in plants waterlogged for 2, 4, and 6 days, respectively, compared to the control (Fig. 2B).

SPAD reading which is the indicator of the chl content of the leaf, showed a lower value in the leaves of waterlogged plants compared to the control plants. In case of the vegetative stage, only 6 days of waterlogging reduced the SPAD values (13%), whereas at reproductive and maturity stages, even 2 days of waterlogging showed a lower SPAD reading and gradually declined with the increment of stress duration. At vegetative stages, 23, 30, and 37%, and at maturity stage 12, 16, and 19%, lower SPAD values were recorded after 2, 4 and 6 days of waterlogging, respectively (Fig. 2C).

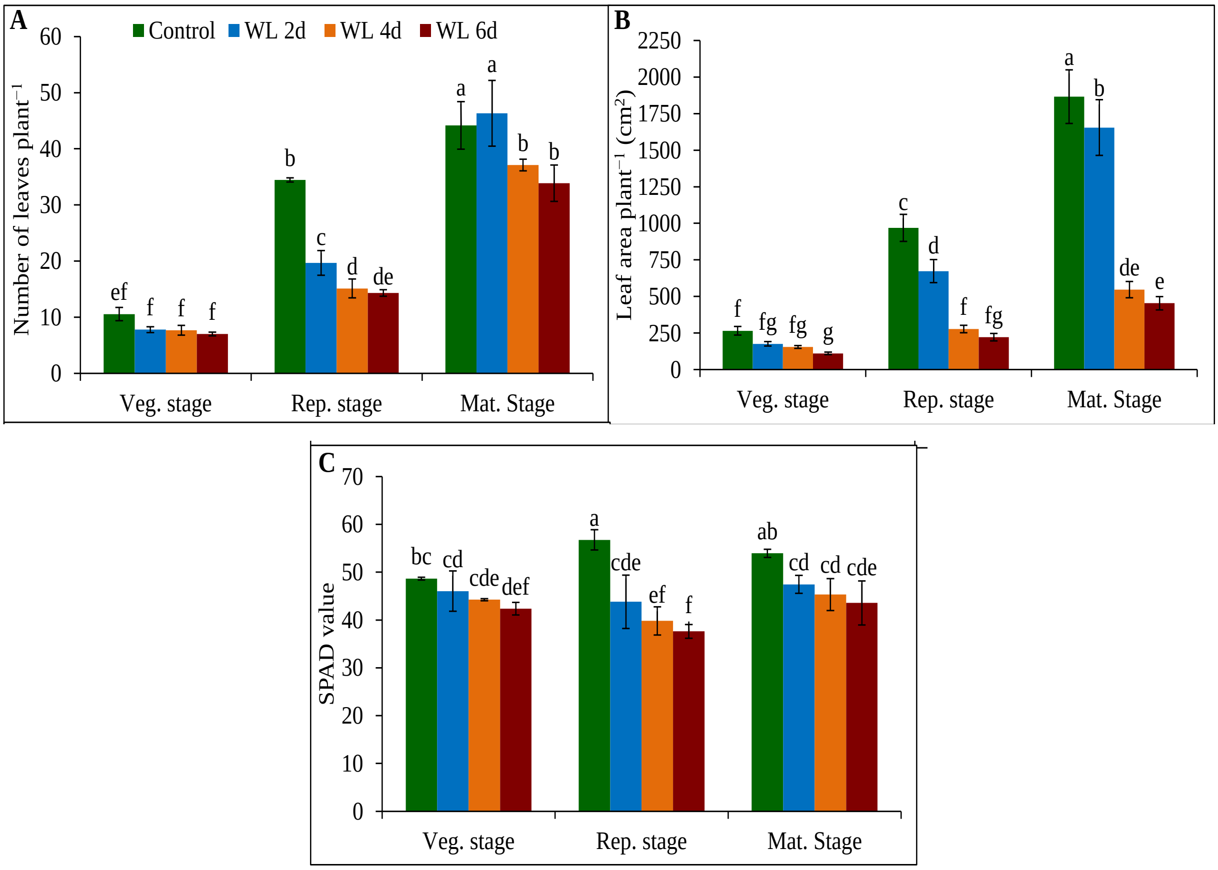

Fig. 2. (A) Number of leaves plant^{-1}, (B) leaf area plant^{-1}, and (C) SPAD value of leaves affected by different durations of waterlogging at different growth stages in sesame crop. Mean (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

Waterlogging significantly reduced the number of capsule plant^{-1} irrespective of the stage and duration at which waterlogging was imposed. The plant waterlogged for 6 days during the reproductive stage showed the lowest number of capsule plant^{-1} (Fig. 3A), which is about 67% lower than the control plants. For 6 days of waterlogging at vegetative or maturity stages number of capsule plant^{-1} reduced by 59%, and for 4 days, it was 47% in both cases compared to the control plants (Fig. 3A).

In this experiment number of seeds capsule^{-1} reduced when waterlogging was imposed at the maturity stage for 2, 4 and 6 days and at the vegetative or reproductive stage for 6 days (Fig. 3B). However, the number of seed capsule^{-1} after 2, 4, and 6 days of waterlogging stress at the maturity stage was respectively 24, 26, and 30% lower than the control plants.

The lowest value of 1000-seed weight was recorded in plants waterlogged at the reproductive stage for four and six days, which were respectively 21 and 25% lower than the control plants (Fig. 3C). Though waterlogging for only 2 days could not affect the 1000-seed weight much, 6 days of waterlogging did the opposite with the lower values at both vegetative (10%) and maturity (11%) stages.

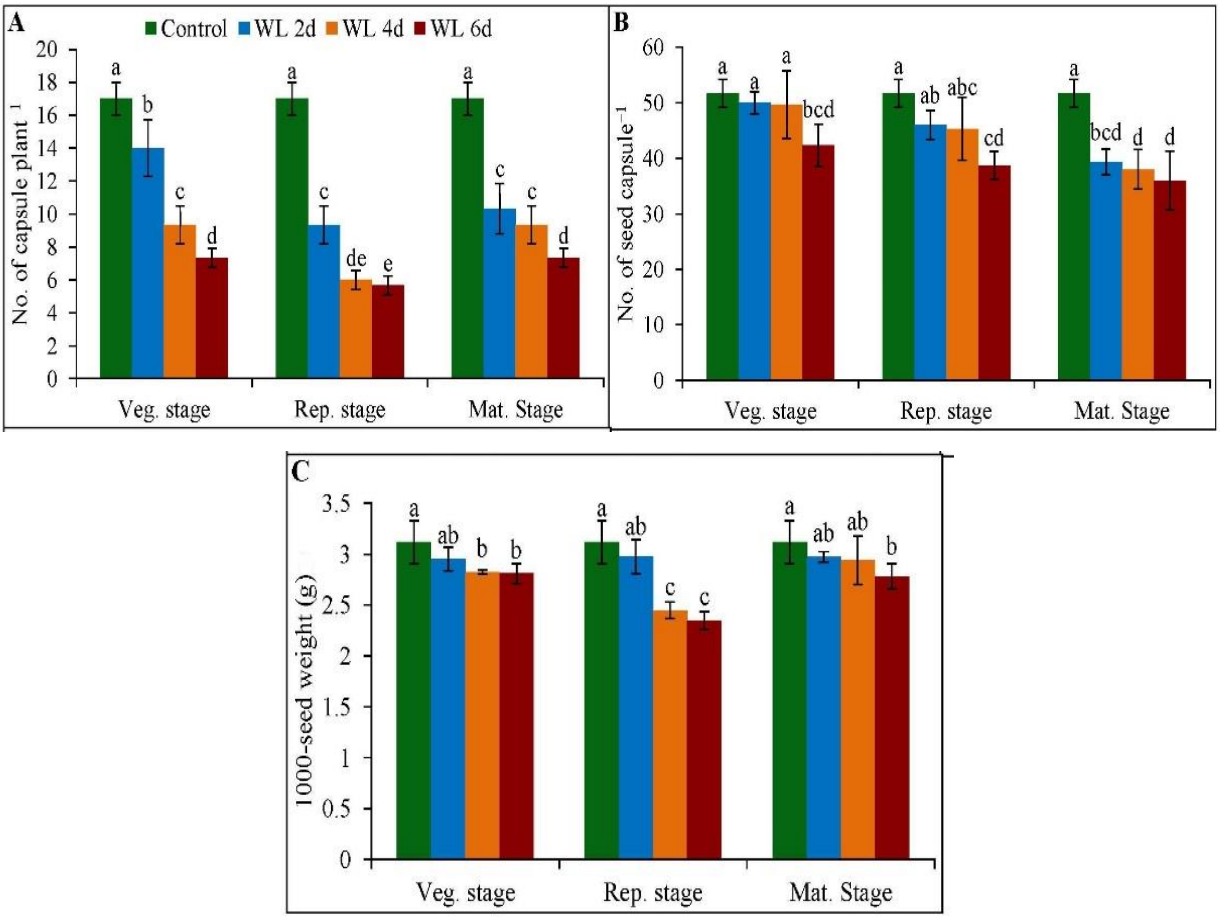

Fig. 3. (A) Number of capsule plant^{-1}, (B) number of seed capsule^{-1}, and (C) 1000-seed weight of sesame affected by different durations of waterlogging at different growth stages. Mean (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test

The highest grain yield plant^{-1} was observed in the control plant, which was greatly reduced by waterlogging treatments irrespective of growth stages. On the contrary, the lowest value (71% lower) of grain yield plant^{-1} was recorded in plants waterlogged for 6 days at the reproductive stage. Two days of waterlogging exposure decreased grain yield plant^{-1} by 31, 54 and 49%, four days of waterlogging by 45, 67 and 55%; and six days of waterlogging by 59, 71 and 68% at vegetative, reproductive, and maturity stages, respectively (Fig. 4A).

Stover yield plant^{-1} also decreased significantly under waterlogging stress compared to well-drained control plants. The lowest value of stover yield was recorded in plants waterlogged for 6 days, with 47, 24, and 37% lower values at vegetative, reproductive, and maturity stages, respectively (Fig. 4B).

Biological yield means the total grain yield and stover yield plant^{-1}, significantly lessened due to waterlogging stress. The longest waterlogging duration (6 days) resulted in 49, 33, and 43% lower biological yield plant^{-1} at vegetative, reproductive and maturity stages, respectively (Fig. 4C).

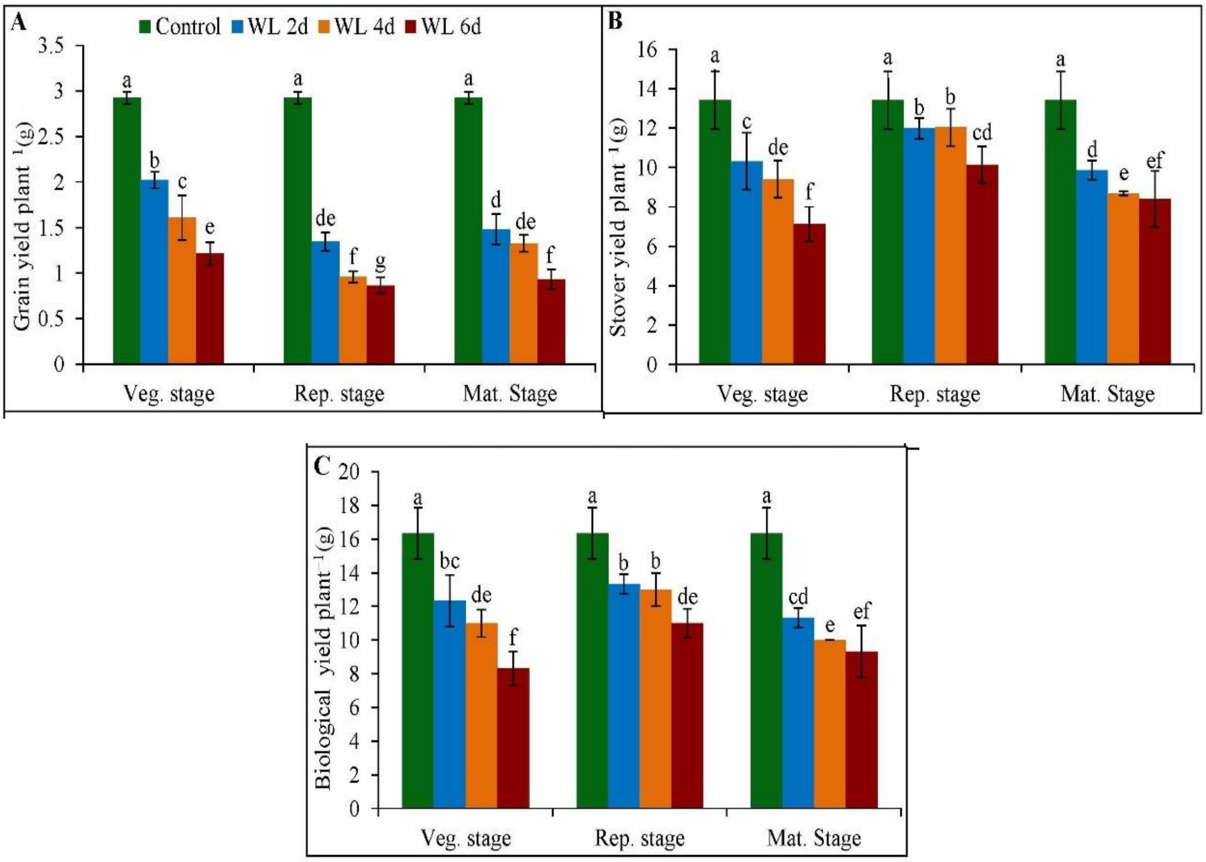

Fig. 4. (A) Grain yield, (B) stover yield, and (C) biological yield of sesame affected by different durations of waterlogging. Mean (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test.

Waterlogging stress can result in a wide array of morphological and physiological alterations leading to yield reduction of sesame (Wei et al., 2013; Saha et al., 2016; Linh et al., 2021). Moreover, available literature on sesame grown under environmental adversities has forecasted significant yield losses, which may threaten global food security. Therefore, a detailed understanding of sesame responses to abiotic stresses like waterlogging is required. A growth stage-dependent study will facilitate the growers to assume the more critical stage of sesame to keep protected from excess water exposure. So, the study was conducted with the latest variety of sesame available and exposed to waterlogging for 2, 4, and 6 days at vegetative, reproductive, and maturity stages.

Plant exposure to waterlogging stress causes a major impact on morphology which is evident from the changes in plant height, above-ground FW, DW, number of leaves plant^{-1} and leaf area plant^{-1}. According to the morphological parameters measured in this experiment, the reproductive stage showed the most susceptibility, and then maturity and vegetative stages, respectively if compared to their respective controls. Such sensitivity of reproductive stages to waterlogging was previously reported in cotton (Wang et al., 2017) and sesame (Linh et al., 2021). Excess water reduces oxygen availability to plant cells, and negative impacts on leaves reduce photosynthesis, so plant growth is hampered. Reduction in plant height of sesame plants under waterlogging or flooding stress was also reported by several other researchers (Mensah et al., 2006; Wei et al., 2013; Saha et al., 2016). Longer durations of waterlogging are prone to wilting, and reduced FW is obtained, and subsequently reduced DW also. Our findings revealed that at vegetative and maturity stages, only 6 and 8 days of waterlogging could reduce the FW and DW of sesame plants, whereas in the case of the reproductive stage, only 2 days of waterlogging significantly reduced sesame FW and DW. Such findings were also reported in cowpea (Olorunwa et al., 2022), barley (Zhang et al., 2007), and sesame (Mensah et al., 2006; Linh et al., 2021). Waterlogging-induced leaf senescence is a major reason for a reduction in leaf parameters. The number of leaves plant^{-1} decreased due to waterlogging stress in cowpea (Olorunwa et al., 2022), soybean (Hasanuzzaman et al., 2022; Sathi et al., 2022) and sesame (Linh et al., 2021). Waterlogging-induced reduction of leaf area was also previously reported in barley (Zhang et al., 2007), mung bean (Kumar et al. 2013), cotton (Wang et al., 2017), cowpea (Olorunwa et al., 2022), soybean (Hasanuzzaman et al., 2022; Sathi et al., 2022) and sesame (Mensah et al., 2006; Saha et al., 2016). Such decline in leaf area can result from photosynthesis reduction due to stomatal closure in waterlogged condition. Other possible reasons are leaf damage, senescence, inhibited leaf formation and expansion, etc. (Olorunwa et al., 2022).

The waterlogging causes denitrification and rapid volatilization, which reduces the available soil nitrogen (N), leading to the lower content of leaf N, limited N-fixation and nodulation (Bacanamwo and Purcell, 1999; Rasaei et al., 2012). Hence, leaf yellowing or chlorosis can result in reduced photosynthetic pigments. The present study documented a duration-dependent declination of SPAD values irrespective of the growth stages (Fig. 2C). However, compared to their respective control reduction, chl was the highest during the reproductive stage which might be due to the greater sensitivity of this stage to excess water. Excess water-induced reduction of leas chl was also documented in several other studies with different crops (Yin et al., 2010; Wang et al., 2017; Hasanuzzaman et al., 2022; Olorunwa et al., 2022; Sathi et al., 2022) including sesame (Wei et al., 2013; Anee et al., 2019; Linh et al., 2021)

Yield is a result of the integration of metabolic reactions in plants. Any factor that influences this metabolic activity at any period of plant growth can affect the yield. Waterlogging stress has shown mostly negative effects on yield attributes (number of capsule plant^{-1}, number of seed capsule^{-1}, grain yield plant^{-1}, stover yield plant^{-1} and biological yield) of sesame plants at different stages and durations. With the increasing duration of waterlogging, the damage effects got higher and at the reproductive stage, it was the most prominent. In some other experiments with sesame plants, a reduction in the number of capsule formation was also evident (Mensah et al., 2006; Saha et al., 2016). The number of seed capsule^{-1} was significantly reduced in sesame plants exposed to waterlogging for 3 days at 29 days after seedling emergence (Saha et al., 2016). Thousand-seed weight was not much affected by a shorter duration of stress, but the longest duration (6 days) of waterlogging reduced all yield attributes. Saha et al. (2016) observed that 3 days of waterlogging stress could not alter the weight of thousand seeds in three sesame genotypes which is also evident in our result for 2 days; even for 4 days when stress was imposed at the maturity stage (Fig. 3C). However, other crops like cotton (Wang et al., 2017), and maize (Ren et al., 2014) have also been studied to have decreased 1000-seed weight under waterlogging stress. Such negative effects of waterlogging stress on the yield of sesame were also demonstrated in earlier studies (Saha et al. 2016).

Conclusion

Sesame is well-known not only for its food values but also for its wide range of adaptability. A crop with multidimensional use and cultivation potential should gain more attention, and waterlogging is one of the major constraints to that task. Our experiment shows that sesame plants exhibit a duration-dependent impairment of their morpho-physiology and yield attributes. Such study of sesame varieties under waterlogging will provide researchers with some important information regarding the response or adaptation mechanisms which will open a new avenue in the way of tolerant variety development. In addition, as the present study demonstrated, the reproductive stage is the most susceptible stage of sesame to waterlogging exposure; growers can use proper agronomic practices to protect the crop during that particular period.

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Author Contributions

T.I.A., with the help of M.H. designed the experiment. T.I.A. performed the experiment, with the active participation of P.K.B. and M.H. M.H. did the statistical analysis. T.I.A. has written the manuscript. All the authors critically reviewed, edited and approved the final manuscript.

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